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RESEARCH ARTICLE

Multiple plumage traits convey information about age and within-age-class qualities of a canopy-dwelling songbird, the Cerulean Warbler

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ABSTRACT

Colorful plumage traits in birds may convey multiple, redundant, or unreliable messages about an individual. Plumage may reliably convey information about disparate qualities such as age, condition, and parental ability because discrete tracts of feathers may cause individuals to incur different intrinsic or extrinsic costs. Few studies have examined the information content of plumage in a species that inhabits forest canopies, a habitat with unique light environments and selective pressures. We investigated the information content of four plumage patches (blue-green crown and rump, tail white, and black breast band) in a canopy-dwelling species, the Cerulean Warbler (*Setophaga cerulea*), in relation to age, condition, provisioning, and reproduction. We found that older males displayed wider breast bands, greater tail white, and crown and rump feathers with greater blue-green (435–534 nm) chroma and hue than males in their first potential breeding season. In turn, older birds were in better condition (short and long term) and were reproductively superior to younger birds. We propose that these age-related plumage differences (i.e. delayed plumage maturation) were not a consequence of a life history strategy but instead resulted from constraints during early feather molts. Within age classes, we found evidence to support the multiple messages hypothesis. Birds with greater tail white molted tails in faster, those with more exaggerated rump plumage (lower hue, greater blue-green chroma) provisioned more, and those with lower rump blue-green chroma were in better condition. Despite evidence of reliable signaling in this species, we found no strong relationships between plumage and reproductive performance, potentially because factors other than individual differences more strongly influenced fecundity.

Keywords: Cerulean Warbler, delayed plumage maturation, honest signaling, melanin, *Setophaga cerulea*, structural coloration, tail white

Múltiples características de plumaje transmiten información sobre edad y cualidades dentro de su clase de edad para un ave canora de dosel, *Setophaga cerulea*

RESUMEN

Las características coloridas del plumaje de muchas aves puede transmitir mensajes múltiples, redundantes, o de poca confianza sobre un individuo. El plumaje puede transmitir información confiable sobre cualidades diversas como edad, condición, y habilidad parental porque tractos discretos de plumas pueden hacer que individuos incurran diferentes costos intrínsecos o extrínsecos. En este estudio, investigamos el contenido de información de cuatro parches de plumaje (corona y rabadilla azul-verde, cola blanca, y franja de pecho negra) en una especie de dosel, *Setophaga cerulea*, en relación a edad, condición, aprovisionamiento, y reproducción. Pocos estudios han examinado el contenido de información del plumaje en una especie que habita el dosel del bosque, un hábitat con ambientes de luz y presiones selectivas únicas. Encontramos que individuos mayores mostraban franjas de pecho más anchas, más blanco en la cola, y coronas y rabadillas con mayor cromía y tonalidad azul-verde (435–534 nm) que los machos en su primer época reproductiva potencial. Por su parte, los individuos mayores estaban en mejor condición (a plazo corto y largo) y eran reproductivamente superiores a los individuos más jóvenes. Sugerimos que estas diferencias de plumaje relacionadas con edad (maduración tardía de plumaje) no fueron consecuencia de una estrategia de historia de vida sino que son resultado de limitaciones durante mudas iniciales de plumaje. Dentro de clases de edad, encontramos evidencia que

apoya la hipótesis de mensajes múltiples. Individuos con más blanco en la cola mudaron sus colas más rápidamente, aquellos con plumaje de rabadilla más exagerado (tonalidad más baja, croma azul-verde mayor) aprovisionaron más, mientras que individuos con croma azul-verde menor estaban en mejor condición. A pesar de evidencias de señales confiables en esta especie, no encontramos relaciones fuertes entre plumaje y desempeño reproductivo, posiblemente porque factores aparte de diferencias individuales tuvieron un efecto mayor sobre fecundidad.

Palabras clave: cola blanca, color estructural, maduración tardía del plumaje, melanina, señalización honesta, *Setophaga cerulea*

INTRODUCTION

Male animals often display secondary sexual ornaments, such as colorful plumage in birds, that convey reliable information about an individual (e.g., condition or genetic quality) during both intersexual and intrasexual interactions (Andersson 1994, Hill and McGraw 2006). These traits may be reliable because only high-quality individuals, or those in good condition, can produce or display the most elaborate plumage (Zahavi 1975). Signals may be complex in many species, and male birds often display multiple plumage ornaments. Several hypotheses have been proposed to explain this phenomenon (Møller and Pomiankowski 1993). First, each individual ornament may reveal different information about the signaler to the receiver (multiple messages hypothesis). Second, multiple ornaments may convey similar information about the signaler to receivers and, together, provide a more dependable expression of quality than any one ornament does alone (redundant signal hypothesis). Third, some ornaments may not actually convey any useful information but instead are simply inexpensive to produce and may exist only because of a preference for them by females, which leads to runaway selection (unreliable signal hypothesis).

Plumage ornaments may provide receivers with reliable information about a variety of condition- or quality-related traits, including the age of an individual (Siefferman et al. 2005, Budden and Dickinson 2009), condition at specific periods (i.e. nutritional status at time of molt; Grindstaff et al. 2012), social status (Rohwer et al. 1981), and parental ability (Germain et al. 2010). While age is an important piece of information that obviously reflects an individual's ability to survive, if plumage coloration evolved via sexual selection (rather than being the result of a life history strategy such as delayed plumage maturation), one would expect to find within-age-class relationships with condition or quality in addition to coarse correlates when age classes are combined (Liffield et al. 2011). Within age classes, various plumage patches can send multiple reliable signals because of the differential intrinsic (e.g., metabolic processes) or extrinsic (e.g., increased intraspecific competition or predation) costs of producing or displaying plumage (Maynard Smith and Harper 2003).

Although investigations into reliable signaling of plumage have become relatively common, there has been little research on the information content of plumage in difficult-to-capture, canopy-obligate species, which have evolved in habitats with different light and selective pressures (Gomez and Théry 2007). When acting as signals, colors must be readily detectable by receivers (i.e. signal efficacy; Andersson 2000), but they must also be cryptic enough to provide necessary camouflage from predators or prey (Endler 1992, Théry 2006, Doucet et al. 2007). Thus, variation in light characteristics of different habitats may have marked effects on the evolution of signaling systems and may also create differential costs of displaying certain plumages, particularly when extrinsic costs exist. Despite these contextual differences, there has been a lack of research on the signaling systems of birds that occupy canopy environments (largely because of difficulty of capture), and current generalizations regarding reliable signaling by plumage are likely biased.

Here, we explore the potential for multiple plumage patches to signal age or act as reliable signals of condition or quality in a canopy-dwelling songbird, the Cerulean Warbler (*Setophaga cerulea*). We test the hypotheses described above and provide one of the first assessments of reliable signaling by an organism living in this unique environment. We evaluate whether four plumage patches—a breast band that typically appears black or dark gray, a blue (or blue-green) forecrown and rump, and white tail patches (Figure 1)—convey messages about male age (second-year vs. after-second-year males), body condition (via body mass and tail-growth bars), parental effort (via provisioning rates), and reproductive performance (via nest success and number of fledglings produced).

METHODS

Study species. Cerulean Warblers are territorial, sexually dimorphic, socially monogamous songbirds that breed in the canopy of mature deciduous forests of the eastern United States (Buehler et al. 2013). They are an appropriate species for exploring relationships between the plumage and quality or condition of a canopy-dwelling songbird because they spend most of their life in the upper canopy, usually in large forest tracts where light conditions (both background and ambient) and selective pressures differ from those of the forest floor or understory, open fields, or

suburban parks (Endler 1993, Théry 2006), where most previous research has been concentrated. In this light environment, Cerulean Warblers have evolved plumage consisting of several distinct patches that may act as reliable signals (Figure 1): They display a black or dark gray breast band, white tail spots (hereafter “tail white”), and unique blue upper-parts (including a bright sky-blue forecrown and blue-green rump). Little research on the color variability or signaling potential of Cerulean Warbler plumage has been done (but see Lyon and Montgomerie 1986). We chose to evaluate these plumage regions because several lines of evidence suggested their importance in signaling and social interactions. We first chose plumage attributes that were known to vary widely among individuals on the basis of literature and evaluation of museum specimens (Buehler et al. 2013, T. Boves personal observation). We also chose plumage patches that we observed to be of importance in the field and in studies of other species. During captures, we observed male Cerulean Warblers investigating the breast bands of decoys, and melanin-based breast patches or stripes have been identified as honest signals and signals of status in other species (Senar 2006). Cerulean Warblers fan their tails in both interspecific and intraspecific interactions, and white tail patches have been identified as signals of quality in other avian species (McGlothlin et al. 2007). The blue forecrown patch was presumed relevant because it is the brightest area of the upper-parts to the human eye, and rump feather coloration is known to differ among age classes (Pyle 1997).

Cerulean Warblers typically have two partial molts per year, and the timing of molt differs by age class (Pyle 1997). Both hatch-year (HY) and after-hatch-year (AHY) birds molt rectrices on the breeding grounds. This happens soon after fledging in the case of HY birds and in mid-July to August for AHY birds. Both age classes then undergo a molt on their Andean wintering grounds, replacing crown, body, and (putatively) rump feathers (Pyle 1997, F. A. Newell personal communication); however, the exact timing of molt is not known. Therefore, we presumed that the plumage patches we assessed were produced either on the wintering grounds (body, crown, and rump feathers) or on the breeding grounds (rectrices).

Capturing birds and morphometrics. We captured male Cerulean Warblers ($n = 55$) breeding in the North Cumberland Wildlife Management Area, Campbell County, Tennessee, USA ($36^{\circ}12'N$, $84^{\circ}16'W$), throughout the breeding season, from early May to mid-June in 2009 and 2010. To capture individuals, we erected mist nets within territories, broadcast territorial songs and call notes, and displayed a male cerulean decoy that was attached to a line and agitated to produce movement. After capture, we aged birds as second-year (SY; first breeding season) or after-second-year (ASY; during or after second breeding season)

on the basis of molt limits (it is particularly useful that SY birds retain some brownish juvenile alula feathers and primary coverts; Pyle 1997). We measured right wing chord to the nearest 0.5 mm (using a straight wing rule) and mass to the nearest 0.01 g (using a digital scale). We fit each bird with a unique combination of plastic colored leg bands to later identify individuals in the field without recapture.

Plumage, condition, parental, and reproductive measurements. In the field, we collected ~ 10 feathers from each individual's forecrown (in front of the eyes) and rump (at the base of the tail, just above the synsacrum) using tweezers. We collected a single tail feather, the first left rectrix (R1), to measure tail growth bars. We stored feathers in glassine envelopes placed inside of coin envelopes in dry, dark, room-temperature conditions. In the field, we took three photographs of each bird. We photographed the breast band by holding the bird with its back flush against a gray piece of cardboard, with a reference ruler placed next to, and at the same depth as, the bird (for calibration purposes). We smoothed the breast feathers and positioned the bill to approximately a 30° angle from horizontal and took photographs using a Nikon Coolpix P5100 12.1-megapixel digital camera. We then took separate photographs of each side of the tail. To do so, we spread the rectrices so that the broad white area on the distal portion of each individual feather was fully exposed. We took tail photographs perpendicular to the surface of the tail and at a distance of ~ 25 cm.

To measure color variables for crown and rump plumage, we formed artificial feather patches (for both rump and crown plumage) by laying feathers on black cardstock paper with minimal reflectance in a manner that mimicked how feathers lay naturally on the bird's body. To determine the minimum number of feathers to use in our patches, we first created test patches using 1–10 feathers for five birds (for both body regions). Total reflectance increased with each additional feather up to four feathers for the rump, and up to five feathers for the crown, so we created all artificial patches using one extra feather for each patch (i.e. five feathers for the rump and six feathers for the crown). We generated reflectance data using an Ocean Optics S2000 fiber-optic spectrometer (range: 250–800 nm; Ocean Optics, Dunedin, Florida, USA). To do so, we held a micron fiber-optic probe, housed within a rubber stopper to exclude all ambient light, at a 90° angle 1 mm from the feather patch. The feather patch was illuminated by deuterium (ultraviolet light source) and tungsten-halogen bulbs (visible-light source). We calibrated the spectrometer prior to data collection and repeated between measurements as needed, using a WS-2 reflectance standard (Labsphere, North Sutton, New Hampshire, USA) for white standardization and by turning off the light bulbs for black standardization. We generated reflectance



FIGURE 1. Three plumage traits of Cerulean Warblers evaluated in this study: (A) blue crown, (B) tail white, and (C) breast band.

data in relation to the standard using OOIBase32 spectral software. We incorporated a smoothing function using a boxcar value of 10, and each data point was the average of 20 spectral measurements. We obtained spectral measurements from three locations on each feather patch at wavelengths between 300 and 700 nm. We averaged data from the three reflectance curves for all analyses. We extracted color variables using the color-analysis software program CLR version 1.05 (Montgomerie 2008) for each of the plumage patches. On average, reflectance for both the crown and rump peaked at ~ 490 nm (blue-green region, hereafter “BG”; Figure 2A, 2B). Variability was greatest in this spectral region, so we calculated BG chroma and BG hue for both crown and rump. BG chroma was calculated as the reflectance ratio $\sum R_i / \sum R_{300-700}$, where i was 435–534 nm. BG hue was calculated as the wavelength of maximum reflectance within the BG region (λR_{\max}). On the basis of research in other birds that display structurally based plumage coloration, Satin Bowerbirds (*Ptilonorhynchus olaceus*; Doucet and Montgomerie 2003) and Tree Swallows (*Tachycineta bicolor*; Bitton and Dawson 2008), we considered males with lower hue (bluer) and greater BG chroma values to display more exaggerated plumage.

To calculate breast band width, we used ImageJ software (available from the U.S. National Institutes of Health at <http://rsbweb.nih.gov/ij/>). We considered the band to consist of the area of dark pigmentation that connected the dark streaking on either side of the bird’s breast (side streaking was not included in our measurements). We calibrated each photo (using the ruler included) and measured the mean vertical width at eight evenly spaced locations along the breast as well as at the maximum and minimum widths. We used the mean breast band width of these 10 measurements as our measure of breast band width. On the basis of research in other birds that display dark breast patches, Great Tits (*Parus major*; Norris 1990, Hegyi et al. 2007) and House Sparrows (*Passer domesticus*; Laucht and Dale 2012), we considered males with wider breast bands to display more exaggerated plumage.

We used ImageJ to measure tail white, which we defined as the mean ratio of white area to the total feather area (across all 12 rectrices). For each individual rectrix (R2–R6

on either side), we used the polygon selection tool to measure the broad white patches at the distal end of each feather, and then did the same for each entire feather. For R1, which we collected, we measured tail white from photographs taken in the lab. We calculated the ratio of white area to total feather area and then averaged that ratio across all rectrices. When possible, we used all rectrices to calculate tail white; however, when one feather was missing or broken, we used only the intact feathers (and assumed that the missing feather had the same amount of white as the complementary feather from the other side of the tail). On the basis of research from another species that displays tail white, the Dark-eyed Junco (*Junco hyemalis*; McGlothlin et al. 2007), we considered males with more extensive tail white to display more exaggerated plumage.

To assess condition at time of capture, we first regressed cubic-root transformed mass on wing length (because wing length is linear and mass is volumetric) and used the resulting residuals as an index of body condition. These residuals were highly correlated to body mass ($r = 0.92$), and because of recent concerns about using unverified indices of body condition, we simply used body mass as our indicator of current body condition (Schamber et al. 2009, Labocha and Hayes 2011). We also performed analyses with both measures and found no change in inference. We evaluated the influence of capture date (Julian capture date and Julian capture date²) on mass and found a negative relationship between capture date and mass ($R^2 = 0.10$, $F_{1, 52} = 5.27$, $P = 0.03$). This relationship was improved only slightly when we also included the quadratic term of Julian date ($R^2 = 0.11$, $F_{2, 51} = 3.10$, $P = 0.05$), so we controlled for capture date by including Julian date alone as a covariate in later analyses.

To gauge condition at time of molt, we used ptilochronology (Grubb 1989). We first measured the collected R1 feather using digital calipers. We then took a digital photograph of the feather under individualized lighting conditions that allowed us to best observe growth bars. Using ImageJ, we measured the average distance between the seven growth bars closest to the proximal end of the feather. We assumed that this distance represented condition at time of tail molt, such that males with more

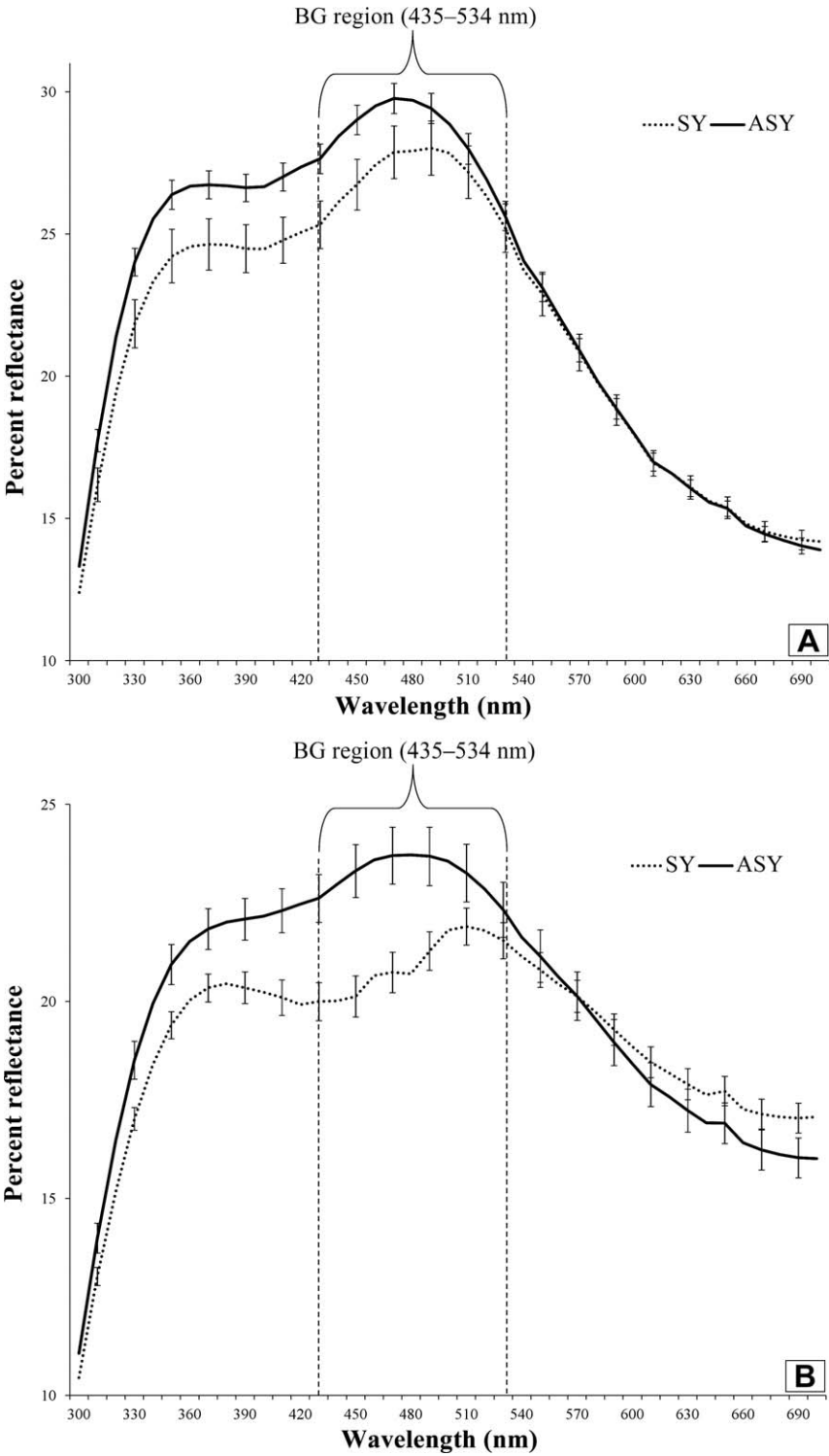


FIGURE 2. Mean (A) crown and (B) rump reflectance curve from second-year (SY) and after-second-year (ASY) male Cerulean Warblers captured in the Cumberland Mountains, Tennessee, USA, 2009–2010. Blue-green (BG) region of spectrum used in analyses is identified. Error bars indicate \pm SE.

nutritional reserves at time of molt would grow tail feathers with wider growth bars (i.e. faster growth; Grubb 2006). Both measures of condition could conceivably be affected by somatic state, as well as by genetic or epigenetic factors (Hill 2011).

Finally, Cerulean Warblers build small open-cup nests high in the canopy of deciduous forests, so we intensively searched for nests between late April and late June in each territory. To find most nests, we first located females and then used behavioral cues to identify the presence and location of the nest. These behaviors included peeling bark off vines, collecting silk, or vocalizing on or near the nest. For a few nests, we used male behavior, including whisper singing or mate feeding, to aid in locating nests. Once a nest was located, we monitored it every 1–3 days to identify the associated male; all nests had only a single male provisioning young. Because of nest height (~20 m on average; see Boves and Buehler 2012), we monitored nests from the ground using spotting scopes equipped with 20–60× zoom lenses; we could not observe contents of nests until nestlings were present, so we used female behavior (i.e. apparent incubation) to infer the presence of eggs. Once incubation began, we monitored nests until successful fledging or nest failure–abandonment was confirmed. When nest failure or abandonment occurred, we searched for renesting attempts (Cerulean Warblers will renest once or twice after failure; Buehler et al. 2013). During days 7–10 of the nestling stage, we monitored nests for >45 min day⁻¹ to count nestlings and fledglings (by day 8, nestlings are restless and quite easy to count). When putative fledging occurred, we searched the vicinity of the nest until we conclusively determined fledging or found the parents engaging in other behavior (such as renesting or solitary foraging). We also recorded each nest for 2 hr during this period, using Sony Handicam video-recorders, and later analyzed video files to measure provisioning rates (feeding visits hr⁻¹ nestling⁻¹). All recordings began between 0700 and 0800 hours on days with little wind and no rain. For males for which we located more than one concurrent nest (i.e. socially polygynous males), we randomly selected one nest to maintain independence. We found no relationship between provisioning rates and the date of the video recording (controlled for paternal age and year; $F_{1, 20} = 1.21$, $P = 0.28$) or the age of the nestlings (controlled for paternal age and year; $F_{1, 20} = 0.68$, $P = 0.42$), so we did not adjust for these factors.

Data analyses. For 10 individuals, a single observer repeated measurements of all plumage patches and assessed the reliability of our field and laboratory methods following Lessells and Boag (1987). We tested for correlations among plumage patches with pairwise correlation tests; because all patches differed among age classes, the latter were partitioned in all tests. For this and subsequent regression analyses, we examined partial

residual versus fitted values, performed Shapiro-Wilk and D'Agostino tests, and examined scatterplots to assess linearity and parametric assumptions. We log-transformed breast band width and crown BG chroma to address issues of non-normality and heteroscedasticity.

We used analyses of variance (or of covariance) to determine whether plumage patches and continuous measures of quality or reproductive performance differed by age class. We used logistic regression to evaluate whether the likelihood of the dichotomous variable nest success (yes or no) differed by age. For all analyses, we treated age, year, and age × year interactions as fixed. We found no significant effect of age × year (all $P > 0.10$), so we removed the interaction term from all analyses. For crown and rump, we performed two tests, one for chroma and one for hue of the BG region. We examined variables for normality (using omnibus test) and equal variance (modified Levene's test); we log-transformed crown BG chroma to address non-normality; all other variables met parametric assumptions. If $P \leq 0.05$, we considered age classes to differ; if $0.10 \geq P \geq 0.05$, we considered age classes to differ marginally.

We used linear regression analysis to assess relationships among plumage traits (dependent variables) and body mass, tail growth, provisioning rates, and number of fledglings (independent variables). We used logistic regression to evaluate the relationship between plumage traits and the dichotomous variable nest success (successful or not across the entire season). To avoid the problems of multicollinearity and differing sample sizes, and because we were interested in comparing the information content of individual plumage patches, we assessed each plumage measurement and independent variable separately. In each analysis, we controlled for age and year by including them as binary independent variables and included all two-way interactions. When interactions were nonsignificant ($P > 0.10$), we removed them from final models. We log-transformed breast band width and crown BG chroma to meet parametric assumptions.

Because we performed multiple tests on each plumage patch, we evaluated our results both uncorrected and using the false-discovery-rate method (Curran-Everett 2000). This method of correcting for multiple comparisons controls for the number of falsely rejected hypotheses (rather than the family error rate) and increases statistical power. We replaced α with a false discovery rate (f_F) of 0.05 that produced a critical significance level (d_i), by $d_i = (i/k) * f_F$ for i of k comparisons, ordered by decreasing magnitude of P values for each independent variable individually (e.g., d_i for independent variable with lowest P value associated with specific plumage patch calculated using $i = 1$, $k = 3$, resulting in a significance level of 0.017; second lowest, $i = 2$, $k = 3$, resulting in a significance level of 0.033, etc.). If the observed significance level (P) was \leq

d_i for a given test, we considered the relationship significant. If $d_i \leq P \leq 0.05$, we considered the result marginally significant; if $P \leq 0.010$, we considered the result to be trending toward significance. For multiple-comparison purposes, we considered analyses involving body mass, tail growth, and provisioning (3 comparisons) to be independent from those involving reproductive measures (2 comparisons). To help visualize the relationship between a plumage patch and any important independent variables, we created partial regression leverage plots (Sall 1990), which depict the relationship between a plumage trait and a single independent variable while controlling for the effect of other independent variables in the multiple regression model (e.g., age and year). We performed all statistical analyses in JMP version 9.02 (SAS Institute, Cary, North Carolina, USA). Values reported in tables are means \pm SE.

RESULTS

Repeatability. All plumage measurements had higher between-individual than within-individual variation (all $P \leq 0.0004$), and repeatability was relatively high in all cases: tail white = 0.91, breast band width = 0.96, rump chroma = 0.67, rump hue = 0.62, crown chroma = 0.50, and crown hue = 0.55.

Pairwise correlations. With age classes pooled, 9 of 15 pairwise correlations were significant (Table 1). With age classes partitioned, correlations were significant only within and between crown and rump color variables. In SY birds, rump BG hue was positively correlated with

crown hue ($r = 0.60$, $P = 0.01$) and negatively correlated with rump chroma ($r = -0.73$, $P = 0.0008$). In ASY birds, rump BG hue was negatively correlated with crown chroma ($r = -0.45$, $P = 0.006$) and rump chroma ($r = -0.56$, $P = 0.0003$) and positively correlated with crown hue ($r = 0.74$, $P < 0.0001$). Crown chroma was also negatively correlated with crown hue ($r = 0.66$, $P < 0.0001$). Within age classes, breast band width and tail white were independent of all other plumage patches; however, measurements of crown and rump were inter-correlated (particularly in ASY birds).

Relationships between plumage and age. Breast band width, tail white, crown BG hue, rump BG hue, and rump BG chroma all differed significantly by age class, and all were more exaggerated in ASY males (Table 2). Body mass and tail growth rate differed significantly by age class, and provisioning rate was marginally different (Table 3). Reproductively, the number of fledglings produced and likelihood of nest success also differed by age (Table 3). All metrics were greater for ASY males. No measure differed by year.

Within-age-class relationships between plumage and quality. After controlling for age (and year), tail white was positively related to feather growth rate at molt, both uncorrected and after applying the false discovery correction (Std Beta = 0.28, $F_{1, 51} = 8.27$, $P = 0.006$; Figure 3A). Rump BG chroma (Figure 3B) and hue were both positively related to provisioning rate, both uncorrected and after applying the false discovery correction (hue negatively: Std Beta = -0.43 , $F_{1, 20} = 8.82$, $P = 0.008$;

TABLE 1. Pairwise correlations (r) between six plumage measurements (see text) for age classes pooled and within age classes in male Cerulean Warblers in the Cumberland Mountains, Tennessee, USA, 2009–2010. Significant correlations at $\alpha = 0.05$ are in bold.

Age class	Breast band width (log)	Tail white	Crown BG chroma (log)	Crown BG hue	Rump BG chroma	Rump BG hue
All ages						
Breast band width (log)	1					
Tail white	0.34	1				
Crown BG chroma (log)	0.12	0.23	1			
Crown BG hue	–0.09	–0.15	–0.56	1		
Rump BG chroma	0.32	0.50	0.25	–0.38	1	
Rump BG hue	–0.26	–0.43	–0.36	0.70	–0.75	1
Second-year						
Breast band width (log)	1					
Tail white	0.04	1				
Crown BG chroma (log)	–0.03	–0.04	1			
Crown BG hue	0.26	–0.11	–0.34	1		
Rump BG chroma	–0.02	–0.06	–0.04	–0.27	1	
Rump BG hue	0.29	–0.02	0.08	0.60	–0.73	1
After-second-year						
Breast band width (log)	1					
Tail white	–0.14	1				
Crown BG chroma (log)	–0.02	0.11	1			
Crown BG hue	–0.08	0.16	–0.66	1		
Rump BG chroma	–0.04	–0.07	0.20	–0.32	1	
Rump BG hue	–0.07	0.050	–0.45	0.74	–0.56	1

TABLE 2. Plumage measurements of breast band width, tail white, rump blue-green (BG) chroma (435–534 nm) and hue, and crown BG chroma and hue for second-year (SY) and adult (ASY) male Cerulean Warblers in the Cumberland Mountains, Tennessee, USA, 2009–2010. In the analyses of variance (ANOVA), we log-transformed crown BG chroma and included age and year as fixed factors. We report untransformed means \pm SE.

Plumage measure	Age		ANOVA	
	SY	ASY	F	P
Breast band width (mm)	1.77 \pm 0.16 Range: 0.90–3.11 (n = 17)	2.44 \pm 0.11 Range: 1.43–3.87 (n = 38)	11.4	0.001
Tail white (%)	14.20 \pm 0.46 Range: 9.13–17.09 (n = 17)	19.11 \pm 0.31 Range: 15.45–23.42 (n = 38)	74.3	<0.0001
Crown BG chroma (%)	31.03 \pm 0.22 Range: 29.36–34.31 (n = 17)	31.60 \pm 0.15 Range: 29.88–32.84 (n = 37)	4.7	0.034
Crown BG hue (nm)	492.07 \pm 3.34 Range: 470–508 (n = 17)	484.26 \pm 2.27 Range: 451–513 (n = 37)	3.6	0.064
Rump BG chroma (%)	27.31 \pm 0.23 Range: 25.08–28.80 (n = 17)	29.00 \pm 0.15 Range: 26.86–30.97 (n = 38)	36.2	<0.0001
Rump BG hue (nm)	516.04 \pm 3.56 Range: 487–539 (n = 17)	494.23 \pm 2.38 Range: 461–523 (n = 38)	24.8	<0.0001

chroma positively: Std Beta = 0.35, $F_{1, 20} = 7.82$, $P = 0.01$). After controlling for age, year, and date of capture, rump BG chroma was negatively related (marginally; not significant after adjusting for false discovery) to body mass (Std Beta = -0.26 , $F_{1, 49} = 5.88$, $P = 0.02$; Figure 3C). We found no relationship between log of breast band width (all $P > 0.50$), log of crown BG chroma (all $P > 0.10$), or crown BG hue (all $P > 0.10$) and tail growth, body mass, and provisioning rate. With respect to reproductive performance, only the relationship between BG crown hue and number of fledglings produced trended toward

significance (Std Beta = 0.25, $F_{1, 43} = 3.09$, $P = 0.09$; Figure 3D); no other statistically significant relationships existed between plumage and reproduction (all $P > 0.10$).

DISCUSSION

We found that older (ASY) male Cerulean Warblers displayed more exaggerated plumage than young (SY) males for all plumage patches measured. Within age classes, we found support for the multiple messages hypothesis, in that several plumage patches conveyed

TABLE 3. Measures of quality (body mass, tail growth, and provisioning rates) and reproductive performance (number of fledglings produced and nest success) for second-year (SY) and adult (ASY) male Cerulean Warblers in the Cumberland Mountains, Tennessee, USA, 2009–2010. We included age and year as fixed factors in all analyses; Julian date of capture was included in body mass analysis. We report untransformed means \pm SE.

Measure	Age		Statistics	
	SY	ASY	F or χ^2	P
Body mass (g)	9.2 \pm 0.1 Range: 8.5–9.8 (n = 17)	9.5 \pm 0.1 Range: 8.8–10.4 (n = 37)	9.8	0.003
Mean tail growth (mm)	2.46 \pm 0.03 Range: 2.23–2.69 (n = 17)	2.64 \pm 0.03 Range: 2.30–3.04 (n = 38)	13.9	0.0005
Provisioning rate (visits hr ⁻¹ nestling ⁻¹)	2.15 \pm 0.44 Range: 1.25–4.33 (n = 7)	2.76 \pm 0.21 Range: 1.50–4.42 (n = 17)	3.3	0.08
Number of fledglings	1.35 \pm 0.41 Range: 0–4 (n = 17)	2.55 \pm 0.30 Range: 0–5 (n = 29)	4.6	0.04
Percentage successfully nesting	41.1 (n = 17)	75.9 (n = 29)	4.8	0.03

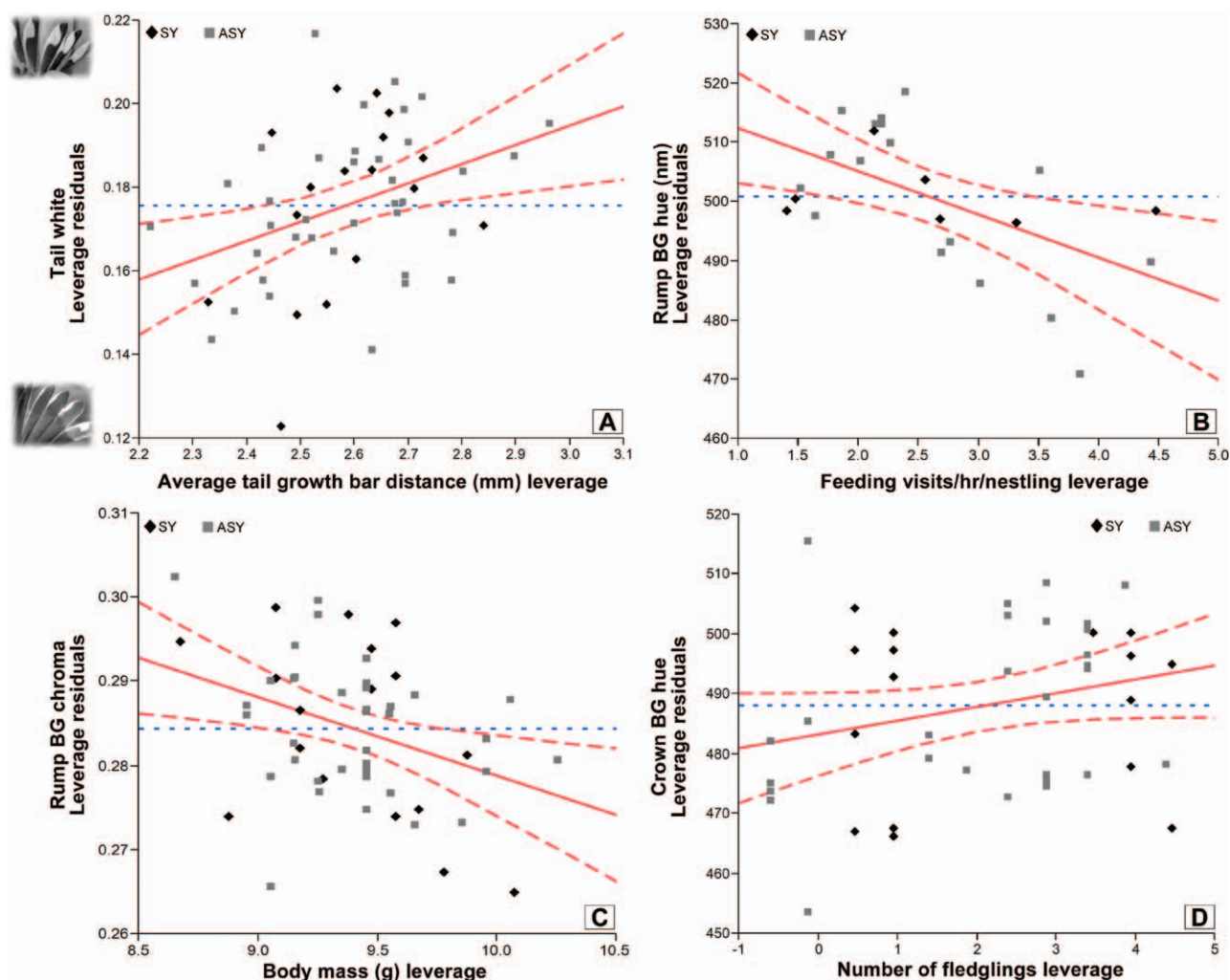


FIGURE 3. Partial regression leverage plots (Sall 1990) for male Cerulean Warblers, indicating relationships (after controlling for age and year) between (A) tail white and condition at molt (via tail growth bars), (B) structural rump blue-green (BG; 435–534 nm) hue and feeding rate, (C) rump BG chroma and body mass (also controlled for date of capture), and (D) crown BG hue and number of fledglings produced in the Cumberland Mountains, Tennessee, USA, 2009–2010. Solid line depicts partial regression line; curved, dashed line represents 95% confidence interval (CI) of partial regression line; and horizontal dotted line represents null hypothesis of no relationship. A CI line that cross horizontal line indicates a partial regression slope different from zero (at $\alpha = 0.05$).

unique information about individuals: Tail white reflected individual condition during the previous breeding season, and rump coloration was related positively to provisioning rate (and negatively to body mass). And crown coloration and breast band width were unrelated to any measure of condition or quality. We discuss each of these results below.

Plumage signals of age. Older male Cerulean Warblers displayed more exaggerated plumage than young males with respect to all patches. Older males also maintained better condition (at time of capture and during molt), tended to feed nestlings at greater rates, and were reproductively superior to younger males. These results suggest that Cerulean Warblers, contrary to Lyon and Montgomerie's (1986) results, exhibit delayed plumage maturation (DPM). However, the delayed plumage matu-

ration that our data show does not appear to be related to the typical adaptive life-history strategy by which subadult birds delay maturation to reduce competition with older males during their first year of life (thereby increasing lifetime fitness; Rohwer et al. 1980). Adaptive DPM typically involves subadult plumage with little or no overlap in coloration between age classes, and/or delayed gonadal maturation (Hawkins et al. 2012), and we did not observe either of these patterns in Cerulean Warblers. Although plumage patches were more exaggerated, on average, in ASY males, several SY males displayed more exaggerated plumage than some older birds for every plumage trait (see range in Table 2). In addition, although SY males were reproductively less successful than ASY males, evidence suggests that this was not due to a lack of

effort. Subadult males (SY) regularly secured mates and (presumably) sired offspring (very few went unmated socially), were prone to intrasexual competition, and responded aggressively to territorial intruders (because this is how we were able to capture them). Some individuals even occupied territories in the highest-density breeding habitat (Boves et al. 2013). Thus, this case of DPM seems more likely driven by constraints at the time of a male's first (for rectrices) or second (for crown, rump, and breast feathers) molt. Constraints may be nutritional, because young birds are inexperienced and inefficient foragers (Wunderle 1991, Desrochers 1992), which, as our provisioning and tail-growth data suggest, may be the case at least into their first breeding season. Additionally, young birds may be prone to increased infection due to delayed immune-system maturation (Buehler et al. 2009), have increased energy costs related to development, or be otherwise handicapped early in life.

Multiple messages within age classes. In support of the multiple messages hypothesis, several plumage patches conveyed unique information about individuals within age classes. Tail white was the only trait that reflected individual condition during the previous breeding season. This may be partly explained by molt schedules. Logically, the production of tail white must coincide with the molt of rectrices, while the production of other plumage patches is temporally decoupled from postbreeding molt and produced up to 3 mo later on the wintering grounds, when individuals may be in different nutritional states. Therefore, potential mates or competitors could assess tail white to gain information about the long-term condition of males. The honesty of tail white as a signal of quality may be enforced via intrinsic and extrinsic costs associated with displaying and maintaining the ornament (Dale and Slagsvold 1996, Qvarnström 1997, Fitzpatrick 1998) and may be particularly relevant in forest canopies, which typically harbor numerous visual predators such as Cooper's Hawks (*Accipiter cooperii*) or Barred Owls (*Strix varia*).

Rump coloration was related to two measures of quality within age classes: positively with provisioning rate and negatively with body mass. Birds that displayed more exaggerated BG hues (i.e. lower wavelengths or bluer plumage) and more exaggerated chroma (greater proportion of their total reflectance in the BG color range) fed nestlings at greater rates. These results support the good parent hypothesis of sexual signaling (Møller and Thornhill 1998). Male Cerulean Warblers provide a large amount of parental care to nestlings, making ~50% of total provisioning trips to the nest (Barg et al. 2006, Boves 2011). Thus, females may benefit by using plumage to assess the resources that a potential partner might provide offspring. Interestingly, although we found that birds with greater BG chroma values provided more parental care,

this color variable was negatively related to body mass, which may suggest that some individuals devote more energy to parental care than to self-maintenance. By the nature of the measurement, chroma in one region of the spectrum is often negatively related to that of other regions, so it is possible that a portion of the reflectance spectrum was positively related to body condition (potentially associated with a secondary peak in the ultraviolet region; Figure 2A), and future research should investigate this possibility.

Despite the positive correlations between ornament exaggeration and measures of quality, we found little association between plumage and reproductive performance (within age classes). There are several potential (not mutually exclusive) explanations for this lack of a relationship. First, we conducted this work during two very productive breeding seasons (nest success was >60% at these sites; Boves and Buehler 2012), and individual differences may not have had a large influence on reproductive output during these years. In years when nest failure is potentially less stochastic and individual traits are more influential, these relationships may be more pronounced. Supporting this supposition is that despite a lack of statistical significance, most relationships between ornamentation and reproductive performance were positive (i.e. birds with more exaggerated plumage tended to be more successful reproductively, although this was not statistically significant). Additionally, forest structure, which varied greatly among territories because of timber harvests in the study area, may have been more influential to reproductive success than individual characteristics (Boves et al. 2013), and this variability may have masked any relationship between individual plumage traits and reproduction. Finally, it is possible that our measures of reproductive performance are misleading because extra-pair paternity may be common in this species (Barg et al. 2006). If birds with less exaggerated ornaments were cuckolded more often by individuals with highly exaggerated ornaments, a relationship between ornaments and reproductive output may, in fact, have existed, but we would not be able to detect it without detailed paternity records. It will be challenging to determine paternity for large numbers of offspring in this species because Cerulean Warbler nests are not easily accessible, but it would be useful to further understand these relationships.

In conclusion, we found that male Cerulean Warblers, which live in the unique light environment of the forest canopy, display multiple plumage patches that provide reliable information on a variety of phenotypic traits, including age, condition, and parental ability. In the future, investigations into how specific environmental conditions in the canopy (light and otherwise) have influenced the evolution of these plumage traits would be interesting. Additionally, studies that focus on other species in

underrepresented environments are needed so that we can better understand how plumage and avian signaling systems vary across habitat types.

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